

Putting Two Water Transport Models to the Test under Wet and Dry Conditions

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Abstract

In order to improve fruit quality and quantity, accurate monitoring of the water status is necessary. The water status can be continuously predicted by using a mechanistic water transport and storage model (e.g. Steppe et al., 2006; 2008). This model typically links measurements of sap flow rate (SF) and stem diameter variations (D) to simulate stem water potential (Ψ_{stem}), which is recognised as one of the best indicators for evaluating plant water status. Despite good model performance under sufficient water availability, the model fails under dry conditions. However, a proper simulation of water transport under drought is essential for many applications. For example, grapevines are often subjected to some level of drought stress during the growing season in order to improve the quality of the grapes. Therefore, we aim at adjusting the existing model to improve its performance in simulating water transport during drought conditions. First, a dynamic function describing changes in hydraulic xylem resistance is used to replace the former constant parameter, and represents the resistances encountered in the soil, root and stem (R^X). Second, also the former constant radial flow resistance between xylem and storage tissues has been replaced by an equation (R^S). For the first time, equations for R^X and R^S instead of parameters were used in the model, and simulations were compared to the original ones. Both models functioned well under wet conditions, but where the original model failed under dry events, the adapted model could still accurately simulate D and Ψ_{stem} under these conditions. The adapted model is thus capable of describing the grapevine's hydraulic response to both wet and (severe) drought conditions and seems very promising within the context of an automatic plant-based system for water status monitoring.

INTRODUCTION

The plant's water status strongly influences fruit quality and quantity in plants and trees (Naor, 2006; De Swaef and Steppe, 2010; Keller, 2010). An accurate monitoring of the water status is thus needed in order to be able to improve quality, which is preferably achieved by measuring on the plant itself (e.g. Jones, 2004). In this respect, mechanistic modelling in combination with plant measurements is very promising, as was illustrated by Steppe et al. (2008). This model links measurements of sap flow rate (SF) and stem diameter variations (D) to simulate stem water potential (Ψ_{stem}), a plant variable assumed as one of the best indicators for evaluating plant water status (Choné et al., 2001; Fereres

and Goldhamer, 2003). The model performs well under well-watered conditions, but fails when used under drought conditions. Nevertheless, good model performance under such circumstances is of utmost importance for many applications, including grapevines (*Vitis vinifera* L.), the species we focus on in this study. Indeed, they often experience drought during the growing season (Gaudillère et al., 2002). Slight-to-moderate levels of drought stress are even applied to improve the composition (and thus quality) of the grapes and resulting wines (e.g. Keller, 2010).

Two aspects might be considered when aiming at developing a model that performs well under drought conditions. First, when water flows along the soil-plant-atmosphere continuum it experiences a hydraulic resistance in each compartment (soil, roots, stem, leaves). The relationship between Ψ_{soil} at a certain distance from the roots (where it is measured) and Ψ_{root} at the root surface (where water is actually taken up by the plant) is a non-linear decrease caused by an increasing water flow resistance of drying soil (Gardner, 1960; Zweifel et al., 2007). Also plant hydraulic resistances are known to increase as the water potential declines due to cavitating xylem vessels (Sperry et al., 1998; Lovisolo et al., 2010). Furthermore, recent findings suggest that aquaporins (water channel proteins) are involved in the regulation of upward water transport by up- or down-regulation of their activity or abundance (Cochard et al., 2007; Lovisolo et al., 2010; Steppe et al., 2012), thereby affecting hydraulic resistance. The latter is especially important for fine roots and leaves (Cochard et al., 2007). In summary, assuming constant soil- and plant hydraulic resistances in water transport models will lead to incorrect simulations under drought conditions. However, current water transport models still use constant resistances (Zweifel et al., 2007; De Pauw et al., 2008; Steppe et al., 2008; De Swaef and Steppe, 2010). Second, besides their role in upward water transport, aquaporins are suggested to influence radial water transport as well (Steppe et al., 2012). As a consequence, the generally assumed constant radial hydraulic resistance between xylem and storage R^S (Génard et al., 2001; Steppe et al., 2006; De Swaef and Steppe, 2010; De Schepper et al., 2011), should actually be variable.

The aim of this study was to implement the above two findings into the original water transport and storage model (Steppe et al., 2006), i.e. adjusting the model in the sense that upward and radial hydraulic resistances are described by a function instead of using a constant parameter value. Therefore, four potted grapevines were monitored continuously and exposed to drying soil conditions by withholding irrigation. Subsequently, model performances of the adapted and original model were compared for wet as well as pronounced drought conditions.

MATERIALS AND METHODS

Plant Material and Experimental Set-up

Data from four potted two-year-old grapevines (cv. Chardonnay) obtained during the 2012-growing season were used for model performance comparison. Plants were grown in the greenhouse facilities of the Faculty of Bioscience Engineering at Ghent University, Belgium. Diameters at stem base ranged from 9 to 17 mm at the beginning of the growing season. The plants were irrigated at least twice a week during the control periods to ensure adequate water availability. Afterwards, the grapevines were subjected to a drought treatment to expose the plants to decreasing Ψ_{soil} . For three grapevines, the period of drought lasted from 11 till 28 June 2012 (DOY 163 – 180), while irrigation was withheld from a fourth grapevine between 21 May and 7 June 2012 (DOY 142 – 159).

Relative humidity (RH) was measured with a RH sensor (Type Hygroclip, Rotronic, Hauppauge, NY, USA), air temperature with a thermocouple (Type T, Omega, Stamford, CT, USA) and photosynthetic active radiation with a quantum sensor (LI-190S, Li-COR, Lincoln, NE, USA), installed near the grapevines approximately 2 m above the ground. Ψ_{soil} of each grapevine was measured using an electronic tensiometer (Type TensioTrans Model 1000 C, Tensio-Technik, Geisenheim, Germany).

Physiological Measurements

During the experiments, sap flow rates (SF) and stem diameter variations (D) were monitored continuously on all grapevines. For SF, heat balance sap flow sensors were used (Models SGA10-ws or SGEX-13, Dynamax Inc., Houston, TX, USA), while Linear Variable Displacement Transducers (LVDT, Model LBB 375-PA-100 and transducer bridge 8C-35, Schaevitz, Hampton, VA, USA or model DF5.0, Solartron Metrology, Bognor Regis, UK) attached to the base of the stem were used to measure D. Every few days, Ψ_{stem} measurements were made with a pressure chamber (PMS Instrument Company, Albany, OR, USA) for each grapevine around noon, or on selected days on different occasions during the day. Therefore, one to three leaves per grapevine were covered in plastic bags coated with aluminium foil for at least 2 h prior to Ψ_{stem} measurements (McCutchan and Shackel, 1992).

Model Description

1. Water Transport Models. The model structure and equations are shown in Fig. 1. For a detailed description, we refer to Steppe et al. (2006; 2008). Briefly summarised, the models consist of two components: a dynamic water transport sub-model, which includes the flow path with rigid xylem and the surrounding storage tissue, and a sub-model that deduces the dynamics of D, resulting from both irreversible growth and reversible daily shrinkage and swelling caused by radial water transport (Génard et al., 2001). Only when the turgor pressure Ψ_p^s exceeds a critical wall-yielding threshold Γ , cells grow. Ψ_p^s depends on the radial water flow between xylem and storage compartment. This is derived from the water transport sub-model and, hence, represents the link between both sub-models. When plants start to transpire in the morning, Ψ_{stem} decreases. Consequently, water uptake is induced by the developed difference in water potential between stem and soil. Since water in storage and xylem tissues are hydraulically connected, also stored water can contribute to the transpiration process (Génard et al., 2001; Steppe et al., 2012), causing the stem to shrink.

2. Hydraulic Resistances. In the original model, the hydraulic resistance is assumed constant and represents the resistance in the xylem (R^X). In the adapted model, R^X is replaced by a resistance that changes with changes in soil water potential. R^X represents the resistance of the entire soil-to-stem segment and can be described as follows:

$$R^X = r_1 e^{-\Psi_{\text{soil}}^2} r_2 \quad (1)$$

in which r_1 and r_2 are proportionality parameters depending on the plant and soil characteristics. The original constant hydraulic radial exchange resistance between xylem and storage R^S is now described by a dynamic function:

$$R^S = s_1 e^{-\Psi_{\text{soil}}} s_2 \quad (2)$$

in which s_1 and s_2 are soil and plant specific parameters of the model.

3. Model Simulations. Both models are implemented in the plant modelling software PhytoSim (Phyto-IT, Mariakerke, Belgium). SF and Ψ_{soil} measurements are used as input. Some model parameters are assigned a value beforehand based on literature or direct measurements, while others are calibrated based on (automatic) D and (manual) Ψ_{stem} measurements. In the original model, four parameters were calibrated: C(stem), ϕ , R^X and R^S (Fig. 1). Replacing the parameters R^X and R^S by their respective equation, adds up to six parameters for calibration (C(stem), ϕ , r_1 , r_2 , s_1 and s_2). For model calibration, the automatic search algorithm Simplex is used to minimise the weighted sum of squared errors (SSE) between the measured data and the model simulations.

For both models, two sets of ten-day data were used per grapevine for model calibration: one during a period of sufficient water availability and one during drying soil conditions. Finally, results obtained with the original and adapted model were compared using the objective model selection criterion, final prediction error (FPE), evaluating the model fit and penalising over-parameterised models:

$$\text{FPE} = \frac{\text{SSE}}{N} + \frac{2p\text{SSE}}{(N - p)N} \quad (3)$$

where N is the number of data points and p the number of estimated parameters. The lower the FPE, the better the model.

RESULTS

Model Simulations during Wet Conditions

Fig. 2 illustrates the model simulations during well-watered conditions for one of the grapevines. The other grapevines behaved similar. The original model with constant R^X and R^S , as well as the adapted model with variable R^X and R^S successfully simulated the dynamics of D and Ψ_{stem} (Fig. 2A and B, respectively). All grapevines had a high SF (data not shown) and daily net diameter growth during the control periods, while Ψ_{stem} never exceeded -0.63 MPa. For all grapevines, FPE values indicate that both models perform quite similar during wet conditions (Table 1).

Model Simulations during Dry Conditions

Drought had a pronounced effect on the functioning of the grapevines, causing both SF and D to decline due to decreasing soil water status (Fig. 3A). A similar trend was observed for Ψ_{stem} measurements (Fig. 3B). At the end of the drought period, Ψ_{stem} ranged between -1.18 and -1.35 MPa for most of the grapevines. One grapevine was only mildly affected by drought, resulting in a minimal decline in SF, D and Ψ_{stem} . Where the original model failed to simulate D and Ψ_{stem} , the adapted model accurately simulated both variables under dry conditions (Fig. 3A and B, respectively). These findings are also reflected by the FPE (Table 1), indicating clearly higher FPE values for the original model, except for the one grapevine that was not greatly affected by drought (Table 1, n° 2; both models behaved similar). Overall, calculated FPE for the original compared to the adapted model was 5 to 14 times higher when simulating D, and 5 to 10 times higher when simulating Ψ_{stem} .

DISCUSSION

Until now, dynamic water transport models based on the approach of Steppe et al. (2006) were not capable of simulating D and Ψ_{stem} accurately under pronounced drought conditions (e.g. De Pauw et al., 2008; Steppe et al., 2008; and demonstrated in Fig. 3).

Therefore, two adjustments were made: equations instead of parameters were used to describe R^X and R^S in order to account for the observed increasing hydraulic resistance in the soil-to-stem segment and increasing radial exchange resistance under decreasing Ψ_{soil} , respectively. Once adapted, model performance was greatly enhanced, allowing accurate simulation under drought conditions (Fig. 3, Table 1). The obtained improvements and simulation accuracy are very encouraging for understanding and interpreting drought mechanisms in plants. It makes the adapted model very promising for future applications, such as a tool for automatic water status monitoring or irrigation scheduling.

Under well-watered conditions, both models performed quite similar (Fig. 2, Table 1). This suggests that R^X and R^S are less variable, making dynamic R^X and R^S unnecessary when simulating plant hydraulics exclusively under well-water conditions. Nevertheless, increasing evidence has been found for the dynamic behaviour of both the upward and radial exchange resistance in the water flow pathway (e.g. Tsuda and Tyree, 2000; Cochard et al., 2007; Steppe et al., 2012). Therefore, using dynamic R^X and R^S will better represent actual plant behaviour and will allow us to better understand and simulate plant functioning.

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Tables

Table 1. Comparison of the Final Prediction Error (FPE) for simulations of stem diameter variations (D) or stem water potential (Ψ_{stem}) of the original model with constant parameters for hydraulic resistance in the xylem R^X and radial exchange resistance between xylem and storage R^S , and the adapted model with both variable hydraulic resistances. Four grapevines were compared during well-watered and dry conditions.

n°	FPE for D (mm ²)		FPE for Ψ_{stem} (MPa ²)	
	Constant R^X, R^S	Variable R^X, R^S	Constant R^X, R^S	Variable R^X, R^S
Well-watered conditions				
1	$4 \cdot 10^{-3}$	$4 \cdot 10^{-3}$	$1 \cdot 10^{-2}$	$2 \cdot 10^{-2}$
2	$2 \cdot 10^{-3}$	$2 \cdot 10^{-3}$	$5 \cdot 10^{-3}$	$5 \cdot 10^{-3}$
3	$9 \cdot 10^{-4}$	$1 \cdot 10^{-3}$	$2 \cdot 10^{-2}$	$2 \cdot 10^{-2}$
4	$2 \cdot 10^{-3}$	$2 \cdot 10^{-3}$	$1 \cdot 10^{-2}$	$2 \cdot 10^{-2}$
Dry conditions				
1	$1 \cdot 10^{-2}$	$7 \cdot 10^{-4}$	0.3	$6 \cdot 10^{-2}$
2	$6 \cdot 10^{-4}$	$5 \cdot 10^{-4}$	$5 \cdot 10^{-2}$	$3 \cdot 10^{-2}$
3	$8 \cdot 10^{-3}$	$1 \cdot 10^{-3}$	1	0.1
4	$1 \cdot 10^{-2}$	$2 \cdot 10^{-3}$	0.3	$3 \cdot 10^{-2}$

Figures

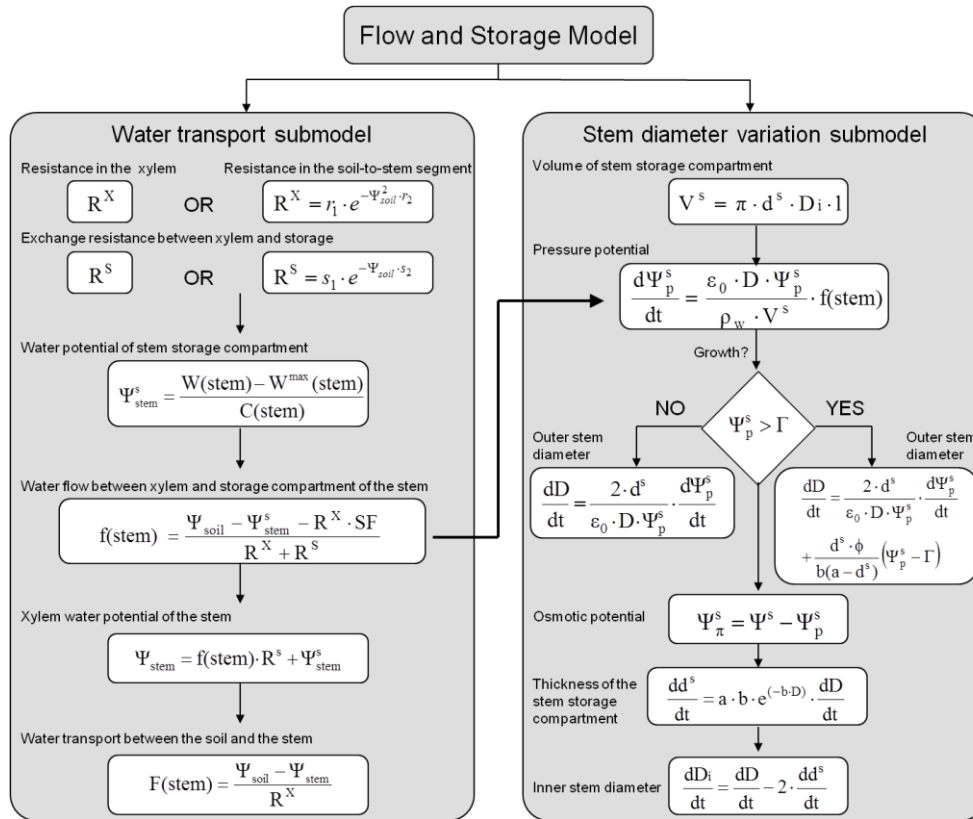


Fig. 1. Schematic overview of the model equations of the original and adapted model. The models consist of two sub-models to link the dynamics of plant sap flow and storage (water transport sub-model) to changes in stem diameter and growth (stem diameter variation sub-model). Following parameters and variables are used in the models: $F(stem)$, water flow between the roots and the stem; Ψ_{soil} , soil water potential; Ψ_{stem} , stem water potential; R^X , flow resistance in the xylem (original model) or flow resistance in the soil-to-stem compartment with r_1 , r_2 , proportionality parameters for calculation of R^X (adapted model); $f(stem)$, water flow between xylem and storage compartment; R^S , radial exchange resistance between the xylem and storage compartment, possibly with s_1 , s_2 , proportionality parameters for calculation of R^S (adapted model); Ψ_{stem}^s , water potential of storage compartment; SF , sap flow rate in the xylem compartment; $W(stem)$, water content of the storage compartment; $W^{max}(stem)$, maximum $W(stem)$; $C(stem)$, capacitance of the storage compartment; V^s , volume of the storage compartment; D_i , inner stem diameter; d^s , thickness of the storage compartment; l , length of the stem segment; D , outer diameter of the stem segment; Ψ_p^s , turgor pressure potential of the storage compartment; ε_0 , proportionality constant; ρ_w , density of water; Γ , threshold at which cell wall-yielding occurs; ϕ , cell wall extensibility; a , b , allometric parameters; Ψ_{π}^s , osmotic potential of the storage compartment.

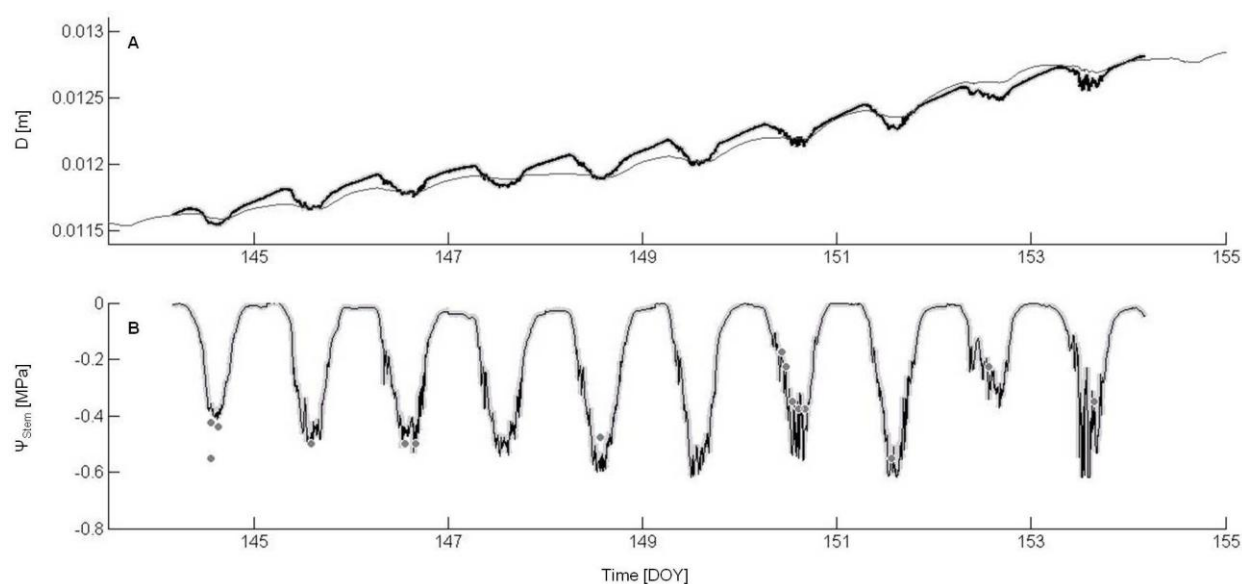


Fig. 2. A typical example of grapevine during a period of sufficient water availability: model simulations of stem diameter variations D (A) and stem water potential Ψ_{stem} (B) with the original model with constant parameters for hydraulic resistance in the xylem R^x and radial exchange resistance between xylem and storage R^s (thick grey lines) and the adapted model with both variable hydraulic resistances (black lines), compared with measured D (thin grey line in A) or Ψ_{stem} (grey dots in B). Time is given in day of year (DOY).

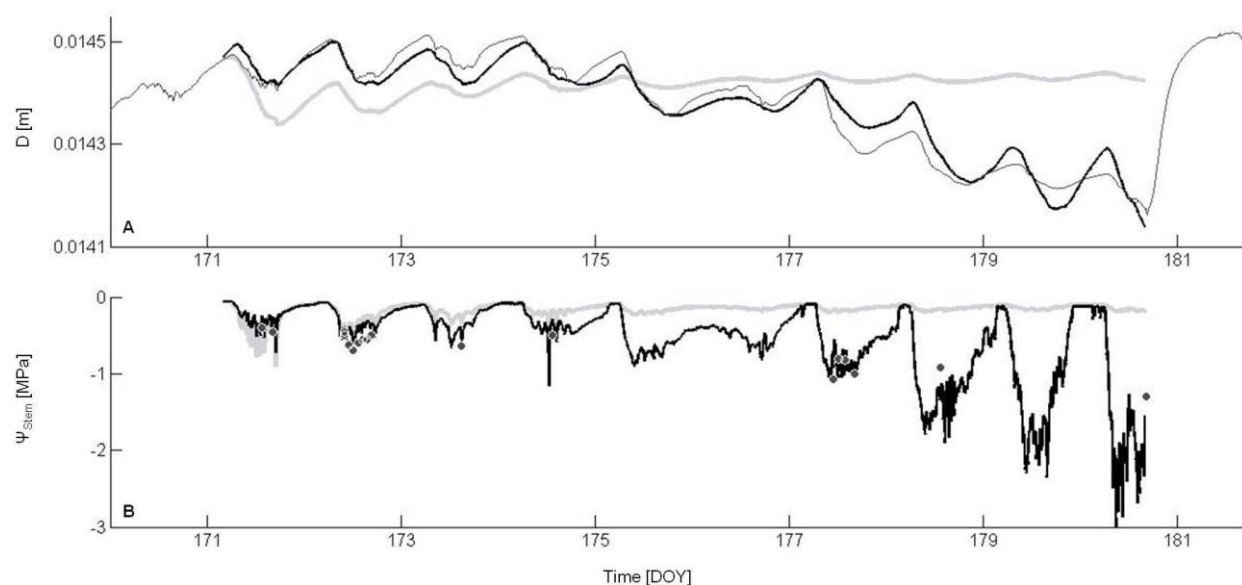


Fig. 3. A typical example of grapevine during a period of imposed drought: model simulations of stem diameter variations D (A) and stem water potential Ψ_{stem} (B) with the original model with constant parameters for hydraulic resistance in the xylem R^x and radial exchange resistance between xylem and storage R^s (thick grey lines) and the adapted model with both variable hydraulic resistances (black lines), compared with measured D (thin grey line in A) or Ψ_{stem} (grey dots in B).